

MICROSTRUCTURE AND GROWTH OF THE CONULARIID TEST: IMPLICATIONS FOR CONULARIID AFFINITIES

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ABSTRACT. The conulariid test has been interpreted as homologous to the theca of coronatid scyphozoans, but recently it has been claimed that the conulariid test and coronatid theca are fundamentally dissimilar. This claim is based largely on putative microstructural characteristics of conulariid tests. Examination of sectioned conulariids using scanning electron microscopy reveals that their microstructure is similar to that of the coronatid theca. Analysis of the microstructure and patterns of malformation of healed injuries and growth abnormalities in conulariids indicates that the conulariid test and coronatid theca were also similar in mode(s) of growth and injury repair. Werner's (1966*a*, 1967) suggestion that the ornamental (outer) layer of the conulariid test is homologous to the outer layer of the coronatid theca is problematic. Nevertheless, the conulariid test and coronatid theca can be interpreted as homologous at a more general level of comparison.

RECENT disagreement over the affinities of conulariids has stemmed in part from conflicting interpretations of the microstructure of the conulariid test. Based on examination of thin sections and/or fracture surfaces, most previous investigators (e.g. Barrande 1867; Bouček and Ulrich 1929; Moore and Harrington 1956*a*; Kozłowski 1968; Bischoff 1978) described the conulariid test as built of microscopic, phosphatic or chitinophosphatic lamellae that parallel the surface of the test. Kozłowski (1968) and Bischoff (1978) showed that conulariid test lamellae are less than 10 μm thick and are alternately dense and vacuity-bearing. They and several other authors (e.g. Barrande 1867; Slater 1907; Bouček and Ulrich 1929) reported that the lamellae are arranged in two layers: an outer layer exhibiting transverse ridges or rows of tubercles (the ornamental layer; Kozłowski 1968), and an inner layer that is more or less smooth (the basal layer; Kozłowski 1968). Moore and Harrington (1956*a*) noted that conulariid tests are often very thin, in some cases as thin as 0.056 mm (56 μm). Several other investigators (Bouček 1928; Reed 1902, 1933; Kowalski 1935; Kiderlen 1937) documented tests that are strongly crumpled but unbroken, or that exhibit regular, inward plication of lappet-like structures at their apertural end. This has been interpreted as evidence that such tests were flexible in life (e.g. Moore and Harrington 1956*a*).

Based in part on similarities between conulariids and thecate polyps of the cnidarian class Scyphozoa, several investigators (e.g. Kiderlen 1937; Bouček 1939; Moore and Harrington 1956*a*; Chapman 1966; Werner 1966*a*, 1967; Bischoff 1978) argued that conulariids were scyphozoans or that they were more closely related to scyphozoans than to any other taxon of comparable rank. These authors interpreted the conulariid test as a mineralized theca, produced by ectodermal tissues covering its inner surface. Taking this hypothesis still further, Werner (1966*a*, 1967) proposed that the conulariid test is homologous to the bilayered theca of coronatid scyphozoans, interpreted by Werner (1966*a*, 1967) as direct descendants of conulariids. Werner (1966*a*, 1967) further suggested that the basal and ornamental layers of the conulariid test are homologous, respectively, to the inner and outer layers of the coronatid theca.

The hypothesis that the conulariid test is homologous to the theca of coronatid scyphozoans has been challenged by several authors (e.g. Kozłowski 1968; Mortin 1985; Feldmann and Babcock 1986; Babcock and Feldmann 1986*a*, 1986*b*), all of whom also reject the hypothesis that conulariids and scyphozoans were closely related. Although none of these investigators has argued that the conulariid test is homologous to the test or theca of some non-scyphozoan group, all have claimed

that the conulariid test and coronatid theca are fundamentally dissimilar. Based on examination of tubercle-bearing conulariid tests, Kozłowski (1968) concluded that the tubercles are pierced by a fine canal (choanophyme) that opens at both the base and summit of the tubercles. Kozłowski (1968) interpreted this canal as the former site of a thread-like sensory organ having no homologue in scyphozoans or any other extant taxon. In order to account for the fact that some of the tubercles he examined lacked an opening at their summit, Kozłowski (1968) further proposed that during ontogeny, choanophymes were covered by deposition of lamellae on the test's exterior surface. This led Kozłowski (1968) to conclude that the conulariid test was secreted internally, rather than externally as in scyphozoans and other cnidarians. (More recently, Babcock (1991) argued that specimens examined by Kozłowski (1968) are not conulariids; however, comparison of Kozłowski's figures with conulariid specimens in collections of the University of Michigan Museum of Paleontology satisfied the present author that Kozłowski's specimens are conulariids.)

Kozłowski's (1968) interpretation of conulariid tubercles as perforated structures was refuted by Bischoff (1973, 1978), who reported (Bischoff 1978, p. 298) that 'sections through tubercles (spikes) of well-preserved conulariid test material have...shown that [test lamellae] are continuous over the whole of the tubercles (and adjacent parts of the test), thus excluding the possibility of the existence of a passageway between the interior [test cavity] and the surrounding medium at any stage.' The feature interpreted by Kozłowski (1968) as a canal opening to the exterior is actually a sharp depression in the basal part of conulariid tubercles, which depression is often revealed through severance of tubercles near their base.

Martin (1985), Feldmann and Babcock (1986), and Babcock and Feldmann (1986a, 1986b) echoed Kozłowski's (1968) conclusion that conulariids represent a group of animals distinct from cnidarians and all other phyla. According to Martin (1985, p. 12), the conulariid test 'displays various features suggestive of a reasonably complex secretory physiology, probably involving a mantle-like secretory mechanism'. In his opinion (Martin 1985, p. 13), this 'seems incompatible with a cnidarian affinity for conulariids'. Feldmann and Babcock (1986) and Babcock and Feldmann (1986a, 1986b) proposed that conulariid tests consist of discrete, solid rods embedded within a finely lamellar integument. In their opinion (Feldmann and Babcock 1986, p. 470), 'the rods and multilayered integument form a style of exoskeletal construction unknown in other organisms'. Based on the purported absence of rods in the genus *Metaconularia* Foerste and the species *Conularina triangulata* (Raymond), two taxa traditionally interpreted as conulariids (e.g. Sinclair 1940, 1948; Wilson 1951; Moore and Harrington 1956b; Van Iken 1991a), Feldmann and Babcock (1986) and Babcock *et al.* (1987) concluded that these taxa are not conulariids. Later, Babcock (1991) interpreted *Metaconularia* as a conulariid, for reasons not specified, but he continued to exclude *C. triangulata* (and, apparently, all other members of the genus *Conularina*) from the group.

Finally, Babcock (1990) documented localized, pearl-like swellings in specimens of *Paraconularia magna* (Ries) from the Pennsylvanian of Oklahoma, USA. Calling these structures pearls, Babcock (1991) concluded that their occurrence in conulariids constitutes evidence of a closer affinity with triptoblastic taxa than with the diploblastic cnidarians.

OBJECTIVES, MATERIAL, AND PROCEDURE

The purpose of the present study is to evaluate the hypothesis that the conulariid test is homologous to the theca of coronatid scyphozoans by addressing recent challenges to this hypothesis by Martin (1985), Feldmann and Babcock (1986), and Babcock and Feldmann (1986a, 1986b), and by making additional comparisons with coronatid thecae. A subsidiary goal of this study is to assess the affinities of *Metaconularia* and *Conularia triangulata*. In addition to covering the microstructure of regular features of conulariid tests, this study also addresses the microstructure and patterns of malformation of healed injuries and growth abnormalities. As recognized by previous authors (e.g. Babcock *et al.* 1987; Mapes *et al.* 1989), such features contain information bearing on the mode of growth of the conulariid test and its relation to former soft tissues.

Conulariids examined for this study range from Ordovician to Pennsylvanian in age and are distributed among six of the twenty-one currently recognized conulariid genera: *Climacoconus* Sinclair, *Conularia* Sowerby, *Conularina* Sinclair, *Metaconularia* Foerste, *Paraconularia* Sinclair, and *Pseudoconularia* Bouček. These six genera include the majority of recognized conulariid species, and they provide a comprehensive sample of basic types of conulariid test ornament. Genera not examined here are known only from steinkerns (e.g. *Anaconularia* Sinclair), are extremely rare and represented by non-preparable type specimens (e.g. *Conulariella* Bouček), or consist of species formerly included within one of the six examined genera (e.g. *Calloconularia* Sinclair, *Notoconularia* Thomas).

Methods. Specimens were examined with the aid of an Hitachi S-570 scanning electron microscope. At relatively low magnifications ($< 1000\times$), best results were given by backscattered electron imaging of polished sections, while at higher magnifications best results were obtained using secondary electron imaging of fracture surfaces. The conulariids, all partial specimens broken at both ends, were embedded in Titan casting resin and then sectioned parallel or perpendicular to their long axis. Sections were ground and polished using 600 grit and $0.3\text{ }\mu\text{m}$ aluminium oxide powder, and then cleaned ultrasonically and coated with gold or carbon. All sections are housed in the Museum of Paleontology of the University of Michigan, Ann Arbor, USA, under collection number UMMP 60000. Other specimens referred to in this paper are repositied in collections of the State University of Iowa, Iowa City, USA (SUI).

REVIEW OF CONULARIID GROSS ANATOMY

As conceived by the present author, conulariids are characterized by an apatitic, steeply pyramidal test that usually exhibits four (but in some cases three or six) sides, or *faces*. More or less complete specimens range from less than two to about 20 cm long, though some taxa (e.g. *Metaconularia papillata* Hall; Middle Ordovician, New York, USA) attained lengths of at least 50 cm. At the test's wide end, called the *aperture*, the faces project beyond the ends of the corners, forming a subtriangular or rounded *lappet* that may be folded over the aperture, covering it (Bouček 1928; Reed 1902, 1933; Kowalski 1935; Kiderlen 1937). Tests whose apical end is preserved exhibit a small (less than 1 mm wide), collar-like holdfast (Kozłowski 1968). Other tests, broken some distance above this site, terminate in a smooth, finely lamellar transverse wall, generally referred to as the *schott*.

Tests of almost all conulariids are crossed by numerous transverse ridges, called *transverse ribs*, or by transverse rows of minute, closely-spaced *tubercles*, which are also arranged in longitudinal files. On each face, tubercle rows and, in most cases, transverse ribs arch toward the aperture. As shown by longitudinal sectioning (e.g. Holm 1893; Sinclair 1948), transverse ribs are an expression of trochoidal or sinusoidal corrugation. Transverse ribs of several taxa (e.g. *Conularia*) bear a single row of closely-spaced, hemispherical swellings, similar to the tubercles of taxa lacking transverse ribs. In the former taxa, the region between two adjacent transverse ribs, the *interspace*, often exhibits longitudinal corrugation.

In nearly all conulariids, the corners of the test are furrowed by a prominent sulcus or groove, associated in several corrugated taxa (e.g. *Climacocomus* and *Paraconularia*) with disruption and offset of the transverse ribs. Corners of many conulariids exhibit an internal carina (e.g. Knod 1908; Bouček 1939; Van Iten 1991a, 1992). This carina, which in some specimens projects about one-sixth of the way to the opposite corner, is often strongly pigmented and visible through the test.

With few exceptions, the midline of each face is marked by a groove or by offset or deflection of transverse ribs. Midlines of many conulariids exhibit one of several distinct types of internal carina(e) (Van Iten 1991a, 1992). As in the case of corner carinae, internal carinae at conulariid midlines are often strongly pigmented and visible through the faces.

ANATOMY AND GROWTH OF THE CORONATID THECA

Details of the anatomy and growth of the steeply conical, chitinous theca of coronatid scyphozoans

have been discussed by Chapman (1966), Werner (1966*a*, 1966*b*, 1967, 1970, 1974, 1979, 1983), and Chapman and Werner (1972). Reviewing the main points, the theca fully covers the side of the polyp and has been observed (Werner 1970) to grow up to 8 cm long. The theca terminates adorally in a small, closed, disc-like holdfast, cemented in life to rocks or other firm substrates. The theca's oral, or apertural end is open, but during strobilation the polyp often closes this end by secreting a thin, circular operculum.

Examination of sectioned thecae using transmission electron microscopy (Chapman and Werner 1972) revealed that they are built of numerous, 12 nanometre-thick lamellae, separated from each other by an equally narrow gap bridged by minute processes. The lamellae are grouped in two layers: a finely sculptured, outer layer, about 2–4 μm thick; and a non-sculptured, inner layer, locally almost 20 μm thick. The sculptured, outer layer extends the entire length of the theca and exhibits transverse and longitudinal corrugation, expressed externally as low ridges. Line drawings of longitudinal cross-sections in Werner (1970) show the outer layer alternately thickening and thinning, respectively, at the crests and troughs of the transverse ridges. Although not explicitly stated, it is evidently the case that the exterior surface of the outer layer (i.e. the exterior surface of the theca) is defined by a single lamella, and that outer layer lamellae below the exterior one run parallel to it and, like it, extend the entire length of the theca.

In contrast to the outer, sculptured layer, the inner layer often pinches out a short distance below the aperture. Measurements made on one specimen (Chapman and Werner 1972), about 30 mm long, showed the inner layer narrowing from a thickness of almost 20 μm near the basal disc to a thickness of 2 μm at a distance of 100 μm from the aperture.

In some coronatids, the inner layer exhibits whorls of eight thorn-like structures that project into the thecal cavity and coincide with the polyp's principal planes of tetrameral symmetry (e.g. Werner 1971, fig. 1; Werner 1983, fig. 2). In all whorls, four of the projections are situated at the base of each of the four gastric septa, which lie in one of the two interradial symmetry planes. The other four projections are situated midway between the interradial ones, in one of the two perradial symmetry planes. The perradial projections are consistently larger (longer, wider, higher) than those at the interradia.

The two coronatid thecal layers also differ in the manner in which they are produced. The outer layer is secreted by gland cells in a collar-like zone of modified ectoderm, the junctional secretory band (Chapman and Werner 1972), that is situated at the polyp's oral end. Werner (1979, p. 85) reported that this structure exhibits 'a small transverse groove in which the soft body and rim [apertural margin] of the tubule are intimately connected'. The gland cells that secrete the outer layer are situated within this rim, and it is their activity that allows the thecal margin to keep pace with the lengthening soft body. Given that lamellae forming the outer layer parallel the exterior surface of the theca and extend its entire length, this implies that the outer layer grows by extension of existing lamellae at the apertural margin.

Production of the inner layer is mediated by gland cells in the side of the calyx, below the junctional secretory band. The inner layer grows by centripetal accretion of whole lamellae. Like production of outer layer lamellae, production of inner layer lamellae occurs throughout ontogeny, resulting in sequential addition of whorls of internal thecal projections (with the basalmost whorl added first and more adorally situated whorls added later).

Especially near the aperture, where the inner layer is absent or extremely thin, the theca is highly flexible. Polyps whose theca has been punctured or severed often repair such damage by depositing a thin patch of inner layer lamellae on the inner surface of the theca.

MICROSTRUCTURE OF THE CONULARIID TEST

Observations

Conulariid tests here examined are built of numerous, extremely thin lamellae, alternately dense and vacuity-bearing, that parallel or are concordant with the surface of the test (Pl. 1; Text-figs 1–2). SEM and X-ray diffraction analysis indicate that the lamellae are composed of cryptocrystalline,

carbonate apatite. To determine if an organic component is present, test fragments were dissolved in 5 per cent hydrochloric acid (see Bischoff 1989); however, no such component (which presumably was present in living conulariids) was recovered. None of the specimens examined here preserved the apex or apertural margin, and thus the number and organization of test lamellae at these sites could not be determined.



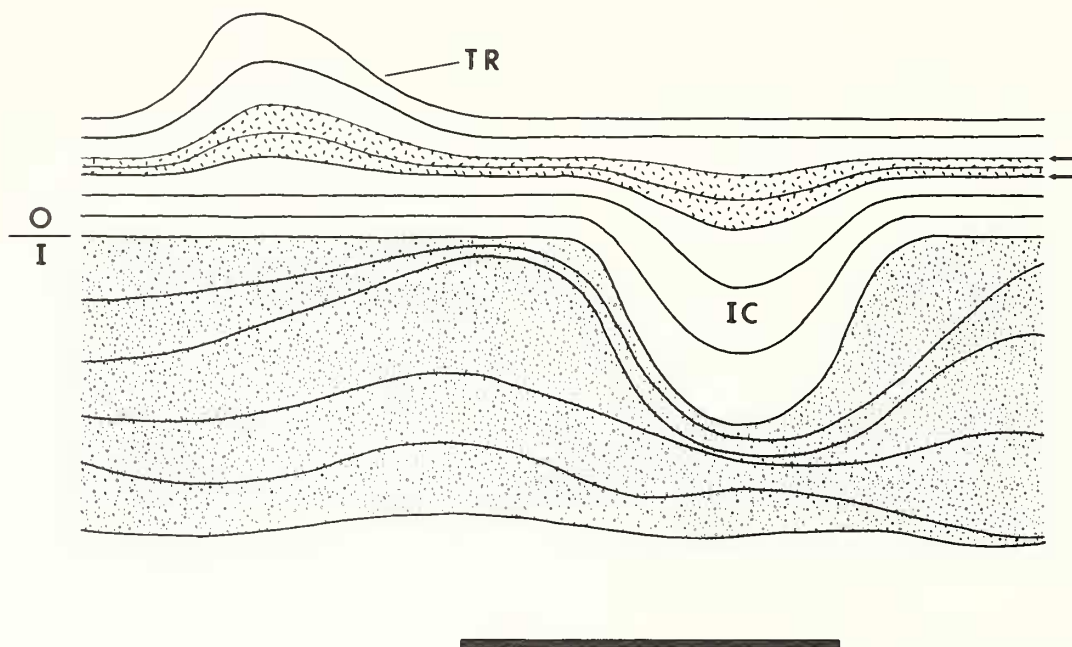
TEXT-FIG. 1. Scanning electron micrographs (backscattered electron mode) of longitudinal sections through conulariid taxa. UMMP 60000. A, *Conularina triangulata* (Raymond); Middle Ordovician, Quebec; note thickening of test lamellae (arrow) in a transverse rib, $\times 420$. B, *Metaconularia* sp.; Middle Ordovician, Galena Group; Illinois, USA; note thickening of lamellae and reduced distinctness of lamellar boundaries in the tubercle, $\times 340$.

Transverse ribs, tubercles and internal carinae, here collectively referred to as test thickenings, represent sites of gradual, symmetrical thickening of individual lamellae (Pl. 1, figs 4–5; Text-fig. 1; see also Van Iten 1991a, fig. 4). Between these sites, lamellae tend to exhibit a uniform thickness of approximately $0.5\text{--}0.7\text{ }\mu\text{m}$ (Pl. 1, fig. 2). Inspection of test thickenings at relatively high magnifications ($> 1000\times$) suggested that lamellae undergoing gradual expansion also split to form additional lamellae.

In some species of *Conularia* and *Paraconularia*, the lamellar fabric is substantially more distinct within the interspaces than within the transverse ribs (Pl. 1, fig. 5). This is due to vacuity-bearing lamellae becoming denser as they pass through the ribs. The same phenomenon was detected in tubercles of *Metaconularia* (Text-fig. 1B), but not in internal carinae.

Relatively thick tests were observed to exhibit two layers, apparently equivalent to the outer (ornamentary) and inner (basal) layers of previous authors (Text-fig. 2). These two layers are particularly distinct in specimens of *Paraconularia crustula* (White), a common species in Pennsylvanian grey shales of the midcontinental United States. As shown schematically in Text-figure 2, the outer layer consists of lamellae that parallel or are in close concordance with the outer or inner surface of the layer, and that participate in the formation of transverse ribs and internal carinae, through gradual, more or less symmetrical thickening. Lamellae participating in the formation of transverse ribs may show reduced distinctness at these sites. Also, whereas lamellae near the outer surface of the layer participate only in the formation of ribs, and those near the inner

surface only in the formation of carinae, lamellae in the central part of the layer may participate in the formation of both types of structures. In contrast to the outer layer, the inner layer consists of lamellae that do not participate in the formation of ribs or carinae, and that often describe irregular, strongly undulatory topographies that are distinctly out of phase with lamellae in the outer layer.



TEXT-FIG. 2. Schematic diagram of part of a transverse section through *Paraconularia crustula* (White). The section passes through a transverse rib (TR) and an internal carina (IC) at a midline. Shown in the diagram are selected lamellar boundaries in a specimen exhibiting highly distinct outer (O) and inner (I) layers. Lamellae in the central part of the outer layer (stippled region marked by arrows) often participate in formation of both ribs and carinae. Diagram based on tracing of individual lamellae in SEM photomicrographs of polished sections through several different specimens. Scale bar = 1 mm.

Discussion

These observations are generally consistent with traditional descriptions of conulariid test microstructure (e.g. Bouček and Ulrich 1929), but they contradict more recent characterizations offered by Feldmann and Babcock (1986) and Babcock and Feldmann (1986a, 1986b). Feldmann and Babcock (1986, p. 469) proposed that conulariid tests consist of 'two separate components', termed integument and rods. Rods are described (Feldmann and Babcock 1986, p. 469) as 'solid, narrow, elongate structures covered by a somewhat flexible, thin, multilayered integument'. According to Feldmann and Babcock (1986 p. 469), '[it] is the rods that, when covered by integument, form the prominent ridges [transverse ribs] across each face of a conulariid'. These authors also proposed that the rods of some conulariids exhibit short projections, called spines, that are oriented perpendicular to the rods and extend into the interspaces (see Babcock and Feldmann 1986b, fig. 2.2).

This interpretation of conulariid test structure is based on the results of low magnification, reflected light and SEM imaging of test material that was not sectioned (Feldmann and Babcock 1986; Babcock and Feldmann 1986a, 1986b). SEM imaging of sectioned material, discussed above,

shows that features interpreted as rods and spines are actually parts of a single, continuously laminated structure. Even in cases where the core of the rib appears to be more or less solid (e.g. Pl. 1, fig. 5), and therefore superficially like a discrete rod, well-defined lamellae on either side of the core 'abut' against it (as opposed to wrapping around it, as implied by Feldmann and Babcock (1986)), and they can be traced through it. Features interpreted as spines arrayed along the rods (e.g. Feldmann and Babcock 1986, fig. 10) are simply crests of the low ridges associated with longitudinal corrugation of the interspaces.

HEALED CONULARIID INJURIES AND GROWTH ABNORMALITIES

Observations

Conulariids exhibiting healed injuries or growth abnormalities have recently been discussed by Werner (1966a, 1967), Babcock *et al.* (1987), Babcock (1988), and Mapes *et al.* (1989). Such features are here assigned to one of two categories. The first category consists of features that have been interpreted as areas of repaired test breakage sustained below the apertural margin, regarded by some authors (e.g. Bischoff 1978; Babcock *et al.* 1987) as a former growth margin. These features are schotts, discussed at length by Sinclair (1948) and Van Iten (1991b), and features analogized by Babcock *et al.* (1987) with embayed injuries (Alexander 1986) on fossil articulate brachiopods. In this paper, features analogized by Babcock *et al.* (1978) with embayed injuries on brachiopods will be referred to as patches.

As seen in external aspect, schotts and patches consist of a more or less circular area of smooth or concentrically rugose test that is surrounded by, and depressed below, rib- or tubercle-bearing test that has been broken (Text-fig. 3). Patches occur on the side of the test and are more or less planar (Text-fig. 3), while schotts cover the apical end and tend to be outwardly convex (e.g. Wilson 1951, pl. 19). Both features may exhibit a small, imperforate dimple or dimple-bearing protuberance, typically located at or near the centre of the area of non-ornamented test (Text-fig. 3). Inspection of sections through schotts (Van Iten 1991b) revealed that they are finely lamellar and extend along the inner surface of the faces proper, toward the aperture. The lamellae parallel the surfaces of the schott, and show no evidence of thickening or reduced distinctness at sites of transverse ribs or tubercles. This suggests that schotts consist of inner-layer lamellae, discussed above. Inspection of fracture surfaces on patches and adjacent test material suggested that patches are similar in microstructure to schotts, and that like schotts they extend for some distance along the inner surface of the faces proper.

Schotts or patches (or both) have previously been documented in *Anaconularia* (schotts; e.g. Barrande 1867), *Archaeoconularia* (schotts; e.g. Barrande 1867; Bouček 1928, 1939; Wilson 1951), *Conularia* (schotts and patches; e.g. Babcock and Feldmann 1986b; Babcock *et al.* 1987), *Paraconularia* (schotts and patches; e.g. Babcock and Feldmann 1986c; Babcock *et al.* 1987), and *Metaconularia* (schotts; Sinclair 1940; Wilson 1951). In this study, patches were observed on specimens of *Metaconularia* as well (e.g. SUI 53089).

The second category of growth abnormalities consists of features interpreted by Babcock *et al.* (1987) as test breakage structures analogous to scalloped and cleft injuries (Alexander 1986) on fossil articulate brachiopods. As described by Babcock *et al.* (1987, p. 99), scalloped injuries are characterized 'by the truncation of one or a few [transverse ribs]', in a manner resembling an angular unconformity (Babcock *et al.* 1987, fig. 7). In their opinion (Babcock *et al.* 1987, p. 99), scalloped injuries 'represent minor [test] damage' sustained along the apertural margin. Babcock *et al.* (1987, p. 99) interpreted cleft injuries as 'V-shaped incisions' into the test that 'have subsequently been closed by the secretion of [test material]'. In their opinion (Babcock *et al.* 1987), cleft injuries were not necessarily sustained along the apertural margin.

Both scalloped and cleft injuries consist of a subtriangular region of abnormally ornamented test that points toward the apex (Babcock *et al.* 1987, figs 7–8; Text-fig. 4 herein). Typically, the region of abnormal ornamentation straddles a midline and consists of one or more ribs or tubercle rows whose central part arches towards the apex, rather than towards the aperture. In cases involving two

or more ribs (or tubercle rows), the degree of departure from normal patterns of arching decreases towards the apertural end of the injury. The lateral margins of the area of abnormal ornamentation are abutted by normally arching ribs or tubercle rows. In addition, ribs or tubercle rows crossing the most apical parts of areas of cleft ornamentation are offset from normally arching ribs or tubercle rows abutting the cleft. Areas of cleft ornamentation differ from scalloped features in showing slight depression of the test surface below the level of laterally adjacent, normally ornamented test; the difference in elevation decreases toward the cleft's apertural end, where the cleft and normally ornamented test are coplanar. Importantly, examination of sections through cleft and scalloped features yielded no evidence of corresponding disruption of internal test microstructure. Test lamellae were observed to pass beneath these features without truncation, offset, or change in number or structure.

These observations suggest that the distinction between scalloped and cleft features is actually one of degree, rather than underlying cause or process. Thus, sites of scalloped ornamentation could be interpreted as responses to relatively minor episodes of injury or irritation, while clefts could be interpreted as responses to more severe episodes.

Cleft (scalloped) ornamentation has previously been documented on specimens of *Comularia* and *Paraconularia* (Babcock *et al.* 1987). In this study, clefts were observed on specimens of *Metaconularia* as well (e.g. Text-fig. 4B).

Interpretations

Schotts and patches. Features similar to conulariid schotts and patches are produced by members of several extant groups, including *Nautilus*, the gastropod *Caecum*, and coronatid scyphozoans (e.g. Chapman and Werner 1972; Bond and Saunders 1989). Members of these groups occasionally undergo perforation or severance of shell or thecal material, which damage is repaired by deposition of new material on the inner surface of the shell or theca. Conulariid schotts and patches probably originated in a similar fashion. Importantly, no case of repaired perforation or severance involving deposition of lamellae on the outer surface of conulariid tests has ever been found.

Cleft ornamentation. Areas of abnormal shell ornamentation similar to cleft ornamentation on conulariid tests have been observed on shells of fossil articulate brachiopods and fossil and living nautiloids (e.g. Alexander 1986; Bond and Saunders 1989). In *Nautilus*, such features are associated with repair of breaks sustained along the growth margin (Bond and Saunders 1989). As noted above, it has been proposed (Babcock *et al.* 1987) that areas of cleft (scalloped) ornamentation on

EXPLANATION OF PLATE I

Scanning electron micrographs of test microstructure in selected conulariids. Figures 1, 4–5 in backscattered electron mode. UMMP 60000.

Fig. 1. *Conularia* sp. Middle Devonian, Cedar Valley Formation; Iowa, USA; longitudinal section through an interspace, showing alignment of alternately dense (light-coloured) and vacuity-bearing (dark-coloured) lamellae parallel to the outer surface of the test (outer surface facing top of page, aperture towards the right), $\times 270$.

Fig. 2. *Paraconularia crustula* (White). Pennsylvanian; Oklahoma, USA; detail of test lamellae exposed on a fracture surface within an interspace (outer surface of test towards the left), $\times 4000$.

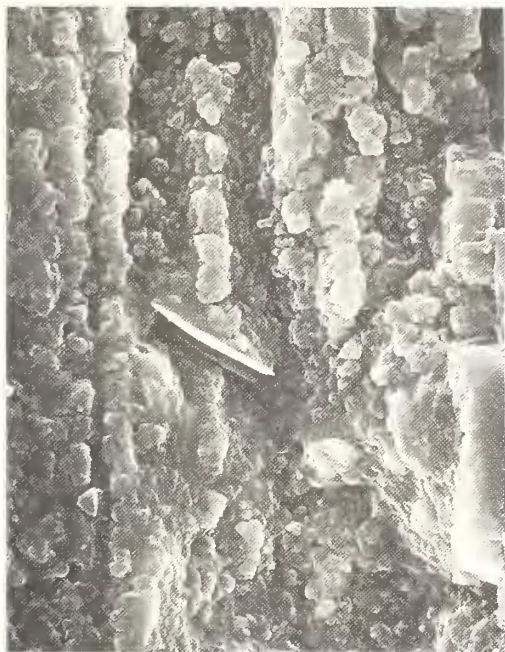
Fig. 3. *Conularia splendida* Billings. Upper Ordovician, Maquoketa Formation; Iowa, USA; view of part of the exterior surface, showing several broken and exfoliated transverse ribs, interpreted by Feldmann and Babcock (1986) as sites of an internal rod distinct from the fine lamellae, $\times 50$.

Fig. 4. *Paraconularia* sp. Mississippian; Illinois, USA; longitudinal section through a transverse rib, showing test lamellae passing through the core of the rib (aperture towards the right), $\times 220$.

Fig. 5. *Conularia* sp. Middle Devonian, Cedar Valley Formation; Iowa, USA; longitudinal section through a transverse rib characterized by reduced distinctness of the lamellar microfabric in the core of the rib (aperture towards the right), $\times 290$.



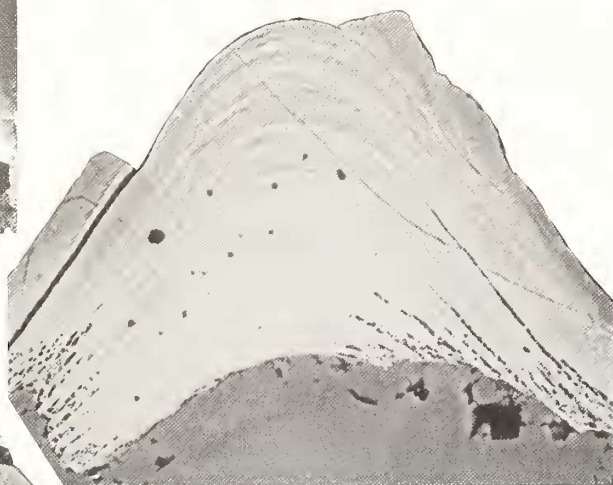
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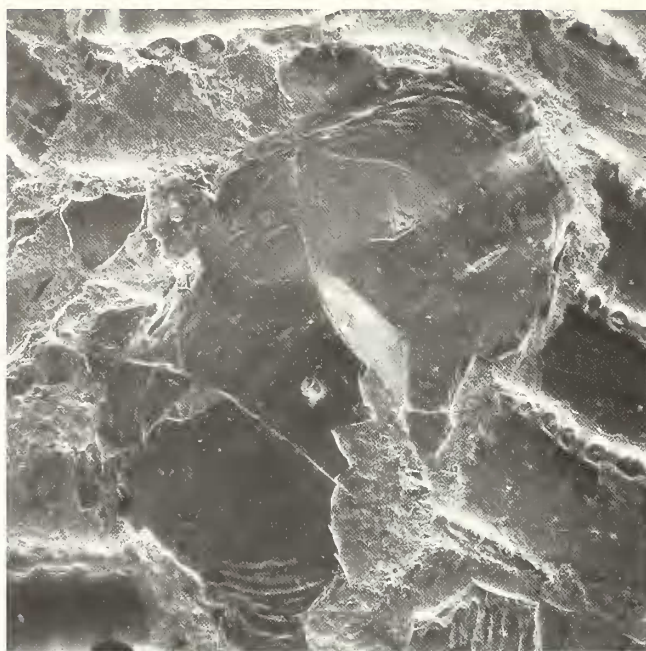
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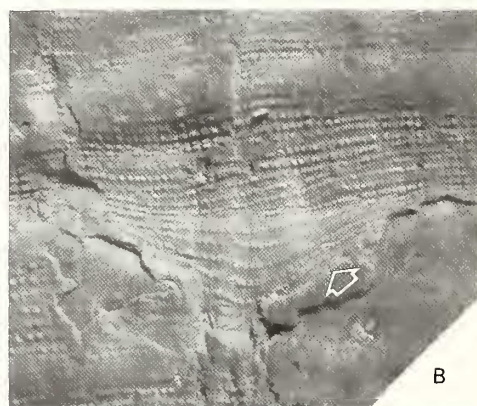
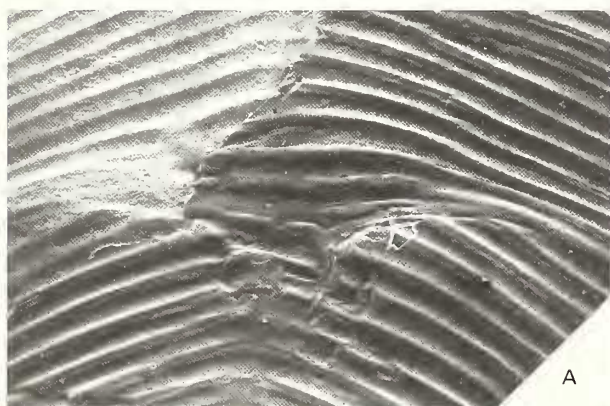
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TEXT-FIG. 3. Scanning electron micrograph of a dimple-bearing patch on a face of *Conularia splendida* Billings; Upper Ordovician, Maquoketa Formation; Iowa, USA; SUI 512a, $\times 20.8$.



TEXT-FIG. 4. Examples of areas of cleft ornamentation on conulariid tests (arrows point to the right lateral cleft margin; photos oriented with the aperture towards the top of the page). A, scanning electron micrograph of cleft ornamentation straddling a midline of *Conularia splendida* Billings; Upper Ordovician, Maquoketa Formation; Iowa, USA; SUI 512b, $\times 25$. B, light micrograph of cleft ornamentation straddling a midline of *Metacomularia* sp.; Middle Ordovician, Galena Group; Iowa, USA; SUI 53089, $\times 5.6$.

conulariid tests represent sites of repaired test breakage. However, no microstructural evidence of repaired test breakage was observed in sections through these features. An alternative interpretation of cleft formation will be presented in the following section.

GROWTH AND RELATION TO SOFT TISSUES

Previous investigators (e.g. Bischoff 1978; Babcock *et al.* 1987) have proposed that growth of conulariid tests involved extension along the apertural margin and centripetal thickening. As noted above, comparisons with extant groups such as *Nautilus* and coronatid scyphozoans indicate that schotts and patches probably represent repair structures produced by soft tissues covering the inner surface of the test. The absence of these or similar features on the outer surface suggests that this surface was not covered by test-producing soft tissues, and thus that the conulariid test is an ectodermal derivative. Schotts (and, probably, patches) are similar in microstructure to the inner layer of relatively thick specimens lacking a schott, further suggesting that growth of the faces proper was at least partly mediated by soft tissues covering the inner surface. The structure and arrangement of lamellae within schotts (patches) and the inner layer indicate that these parts of the conulariid test most likely grew by centripetal accretion of whole lamellae.

The same process may also have formed the outer layer, which has been interpreted by some previous authors (e.g. Bischoff 1978) as a product of extension along the apertural margin. Except for the presence of ribs, tubercles and carinae, lamellae in the outer layer are similar to inner layer lamellae. Moreover, lamellae in the outer layer parallel or are in close concordance with the surfaces of the layer, and the outer layer shows no evidence of microstructural features that could be interpreted as growth lines inclined to the lamellae. To be sure, comparisons with extant groups suggest that areas of cleft ornamentation on conulariids reflect progressive healing of damaged or irritated soft tissues lining a former growth margin. However, the absence of corresponding disruption of internal test microstructure further suggests that the healed soft tissues were not involved in the formation of mineralized test material. How, then, could damage to such tissues be expressed as areas of cleft ornamentation on mineralized conulariid tests? One possibility, consistent with microstructural evidence presented here, is that conulariids possessed a set of weakly or non-mineralized lamellae, situated abaxially to the mineralized lamellae preserved in conulariid fossils and produced by soft tissues lining the apertural margin. Repair of breaks in non-mineralized lamellae or localized irritation of soft tissues that produced them might have led to formation of areas of cleft ornamentation, preserved in conulariid fossils by virtue of non-mineralized lamellae having been underplated by mineralized lamellae. Under this scenario, all of the lamellae in conulariid fossils, including both outer and inner layer lamellae, were accreted, whole, to the inner surface of the non-mineralized layer. Given that mineralized lamellae parallel or are concordant with the test surface, this implies that production of mineralized lamellae began late in ontogeny, after extensional growth along the apertural margin had ceased.

To summarize, the conulariid test is an ectodermal derivative produced by soft tissues covering its inner surface and, possibly, apertural margin. Production of mineralized lamellae involved centripetal accretion of whole lamellae. Although extension along the apertural margin is suggested by the occurrence of cleft ornamentation, such growth may have involved thecal material that was not mineralized.

AFFINITIES OF *METACONULARIA* AND *CONULARINA TRIANGULATA*

As noted above, Feldmann and Babcock (1986) and Babcock *et al.* (1987) proposed that *Metaconularia* and *Conularina triangulata* are not conulariids, based on purported differences in test microstructure. However, results of this study show that *Metaconularia* and *C. triangulata* are similar in microstructure (and, at least in the case of *Metaconularia*, injury repair) to genera regarded by Babcock *et al.* (1987) as conulariids. These taxa also display a number of uniquely shared gross anatomical similarities that further support their assignment to a single, monophyletic

group that excludes other organisms. These similarities include: (1) possession of transverse ribs (e.g. *Conularina triangulata*, *Conularia*) or tubercle rows (e.g. *Metaconularia*, *Pseudoconularia*) that generally arch towards the aperture on the faces (Sinclair 1940, 1942, 1948); (2) possession of sulcate corners (e.g. *Metaconularia*, *Conularina triangulata*, *Conularia*) that may be either non-thickened (e.g. *Metaconularia*, *Pseudoconularia*) or internally carinate (e.g. *Conularina triangulata*, *Climacoconus*, some species of *Conularia*) (Sinclair 1940, 1942, 1948; Van Iten 1991a, 1992); and (3) possession of a distinct facial midline associated internally with a pair of longitudinal carinae or thickenings, with members of each pair situated on opposite sides of the midline proper and diverging toward the aperture (e.g. *Metaconularia*, *Conularina triangulata*, certain *Climacoconus*; Van Iten 1991a, 1992).

COMPARISONS OF CONULARIIDS AND CORONATID SCYPHOZOANS

Together with results of previous studies (e.g. Werner 1966a, 1967; Bischoff 1978; Van Iten 1992), results of the present investigation confirm that the conulariid test and coronatid theca share detailed similarities in microstructure, gross anatomy, and mode(s) of growth and injury repair. These similarities can be summarized as follows:

1. theca constructed of numerous, extremely thin ($< 1 \mu\text{m}$) lamellae that parallel or are in close concordance with the surface of the theca and are alternately dense and vacuity-rich;
2. transverse and longitudinal corrugation of lamellae;
3. localized inflection of centripetally accreted lamellae to produce tetramerally arranged, seriated (coronatids and certain conulariids) or continuous (certain conulariids) internal projections or carinae (Bischoff 1978; Van Iten 1991a, 1992);
4. repair of perforation or severance involving deposition of non-ornamented lamellae on the inner surface of the theca;
5. growth involving centripetal accretion of whole lamellae and, possibly, extension of lamellae along the apertural margin.

As indicated by published discussions of other metazoan taxa (e.g. Jollie 1962; Barnes 1987), some of the similarities (similarities 3 and 5) outlined above are uniquely shared by conulariids and coronatid scyphozoans. The present study yielded no evidence of greater similarity between conulariids and tests or thecae of any non-scyphozoan group (e.g. tubiculous polychaete annelids, ascidians, pterobranchs, molluscs). Localized, finely lamellar internal swellings, similar to the pearl-like structures observed by Babcock (1990) in tests of *Paraconularia magna*, occur in the theca of the coronatid *Stephanoscyphus eumedusoides* Werner (see Werner 1974, fig. 4), and thus Babcock's (1991) suggestion that the occurrence of pearl-like structures in conulariids is inconsistent with a scyphozoan affinity for this group seems unwarranted. Although Werner's (1966a, 1967) suggestion that the outer (ornamentary) layer of fossil conulariids is directly homologous to the outer layer of the coronatid theca may be incorrect, the occurrence of cleft ornamentation on conulariid tests suggests that the theca of living conulariids consisted of two layers, similar in origin to the two layers of the coronatid theca.

To summarize, the hypothesis that the conulariid test is homologous to the theca of coronatid scyphozoans is based on detailed similarities in microstructure and mode(s) of growth and repair of injuries. Opponents of this hypothesis have yet to show that the conulariid test is more similar (and therefore more likely to be homologous) to the test or theca of any non-scyphozoan group. Although differences between conulariid tests and coronatid thecae in shape and degree of mineralization have been interpreted as evidence against homology of these structures (Termier and Termier 1949, 1953; Kozłowski 1968; Babcock 1991), the similarities discussed above suggest that these differences can reasonably be interpreted as reflecting descent with modification from a thecate common ancestor.

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